THE INFLUENCE OF HONEYDEW ON ARTHROPODS ASSOCIATED WITH BEECH TREES IN NEW ZEALAND

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(Received 6 August 1993; revised and accepted 4 October 1993)

ABSTRACT

Didham , R.K. (1993). The influence of Honeydew on arthropods associated with beech trees in New Zealand. *New Zealand Natural Sciences* 20: 47-53.

Arthropods were collected from the crowns of four mountain beech trees, *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole (Fagaceae). Preliminary data based on one 'non-honeydew' tree suggest that arthropod abundance, species dominance patterns and community structure vary markedly between beech trees with a complement of sooty beech scale (*Ultracoelostoma* spp.) and those without. It is implied that scale honeydew secretions provide an essential resource base for arthropods in beech forests and that this is an important factor determining the abundance and composition of the arthropod fauna. In addition, changes in tree morphology brought about by associated fungal mould growth may influence the abundance (and perhaps composition) of certain bark and epiphyte dwelling arthropods. Further data are needed to conclusively demonstrate the role of scale honeydew secretions in determining arthropod community structure in New Zealand beech forests.

KEYWORDS: *Nothofagus solandri* - *Ultracoelostoma* - honeydew - canopy - arthropods - *Vespula* spp. - New Zealand.

INTRODUCTION

Considerable attention has focused on the role of honeydew in the functioning of beech forest ecosystems (Belton 1978, Crozier 1981, Wardle 1984, Moller *et al.* 1987, Moller & Tilley 1987, 1989), particularly its importance to forest birds (Gaze & Clout 1983, Taylor 1985, Boyd 1987, Beggs 1991), honey production (Cook 1971, Crozier 1978) and the invasion of vespid wasps in New Zealand (Harris *et al.* 1991, Harris 1991, 1992, Moller *et al.* 1991). However, the importance of honeydew as a resource for native insects and other arthropods has been almost entirely neglected (Boyd 1987, Moller & Tilley 1989).

The distinctive association of sooty beech scale (*Ultracoelostoma assimile* (Maskell) and *U. brittini* (Morales) (Margarodidae) and sooty mould fungi (*Capnodium, Trichopeltheca* and *Capnocybe* spp.) (Hughes 1972) with *Nothofagus* spp. is an unique feature of New Zealand beech forests. However, not every tree is infested with scale insects. The reasons for this are unclear, but may be related to site microenvironmental conditions or growth characteristics of individual trees (Crozier 1978, Gaze & Clout 1983, Morales *et al.* 1988, Kelly 1990, Kelly *et al.* 1993). McAllum (1992) found that first instar *U. brittini* 'crawlers' did not colonize open bark habitat on 'non-honeydew' beech trees, whereas the colonization rate on experimentally stripped areas of 'honeydew' beech (red beech, *N. fusca* (Hook. f.) Oerst.) was rapid, suggesting that non-honeydew trees lack suitable colonization sites (crevices) for sooty beech scale. The proportion of non-honeydew to honeydew trees varies from location to location, but generally is low (pers. obs.). The presence of trees without scale insects provides an opportunity to isolate the influence of honeydew on the arthropod composition of beech trees.

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This paper is part of a larger study which investigated the composition and spatial heterogeneity of canopy arthropods in a mixed podocarp-broadleaf-beech forest (Didham 1992). One of the four beech trees sampled during the study was, fortuitously, a 'non-honeydew' tree. Subsequent surveys revealed it to be the only non-honeydew tree in the study area. In this paper I report that marked differences in arthropod abundance, species dominance and overall community composition were observed between honeydew beech trees and the non-honeydew tree. While stressing the need for caution in drawing conclusions from limited data, I emphasize the significance of these data for the conservation of beech forest arthropods in the face of an invasion of introduced wasps, and provide suggestions for further research.

MATERIALS AND METHODS

STUDY SITES

Sampling was conducted in the Blue Duck Scientific Reserve, Kaikoura, South Island, New Zealand (NZMS260 P31 GR747855). The forest is a diverse, mixed podocarp-broadleaf stand of approximately 85 ha, interspersed with isolated patches of mountain beech (Wardle 1961, Wardle 1971). Two mountain beech trees were sampled from within each of two patches. Trees B-1 and B-2 were in patch A, and trees B-3 and B-4 were in patch B. Trees within each pair were 29m and 37m apart, respectively, and the two beech patches were 650m apart. B-1, B-2 and B-3 were 'honeydew' beech trees, whereas tree B-4 lacked sooty beech scale (*Ultracoelostoma* spp.). B-4 is referred to here as the 'non-honeydew' beech tree.

SAMPLE COLLECTION

Flight intercept traps (FITs) were placed at a height of 13-15 m in the four beech tree crowns. Each trap consisted of a clear 0.25 m^2 P.V.C. intercept sheet with a collecting tray containing Gault's solution suspended beneath (Didham 1992). Ten weekly samples were collected between November 1990 and February 1991. One sample from B-1 was lost because of high winds, so week 5 data were excluded from analyses. Abundances of each arthropod class and insect order were recorded for samples from the remaining nine weeks. Subsequently, two insect orders, Coleoptera and Diptera (excluding the poorly known families Cecidomyiidae and Sciaridae), were sorted to recognizable taxonomic units (RTUs) present in six of the nine sampling weeks (weeks beginning 13 Nov. (1990), 20 Nov., 27 Nov., 15 Jan. (1991), 22 Jan., and 19 Feb.). Sorting was limited by time constraints. Immature insects were not included in analyses.

ANALYSIS

Dipteran species-abundance data were used to identify differences in species composition between honeydew trees and the non-honeydew tree. Faunal similarity between tree crowns was measured with C_m (Grassle & Smith 1976), a modification of the Morisita-Horn index (Morisita 1959, Horn 1966). C_m overcomes the bias toward common species inherent in the Morisita-Horn index (Grassle & Smith 1976, Wolda 1981), and was considered by Wolda (1983) to be far superior to all other similarity measures.

Detrended correspondence analysis (DECORANA, Hill 1979) was carried out using dipteran species-abundance data on the PC-ORD statistical package (McCune 1991).

RESULTS

VARIATION IN ABUNDANCE AND SPECIES DOMINANCE

A total of 79 795 arthropods were collected from the four beech tree crowns. The (log) abundance of Diptera was significantly lower on the one non-honeydew tree (ANOVA; $F=7.89$, $p<0.001$) (Fig. 1a). A similar pattern was evident for Lepidoptera (ANOVA; $F=16.17$, $p<0.0001$) (Fig. 1b) and Hemiptera (ANOVA; $F=4.39$, $p<0.05$). In the case of Diptera, much of the variation was brought about by two dominant species, *Tetragoneura* sp.A and *T. spinipes* (Mycetophilidae), which were abundant on honeydew beech trees, but not on B-4 (Table 1). In contrast, no significant variation in abundances between tree types was found for Coleoptera (ANOVA; $F=2.54$, $p>0.05$) or Hymenoptera (ANOVA; $F=0.06$, $p>0.05$). Conversely, Thysanoptera (Fig. 1c) and Blattodea (Fig. 1d) were more abundant in the non-honeydew tree crown, although differences among crowns were only significant for Blattodea (ANOVA; $F=6.55$, $p<0.01$).

Honeydew trees were dominated by different species of Diptera to those on the non-honeydew tree (Table 1), and trees exhibited differing dominance

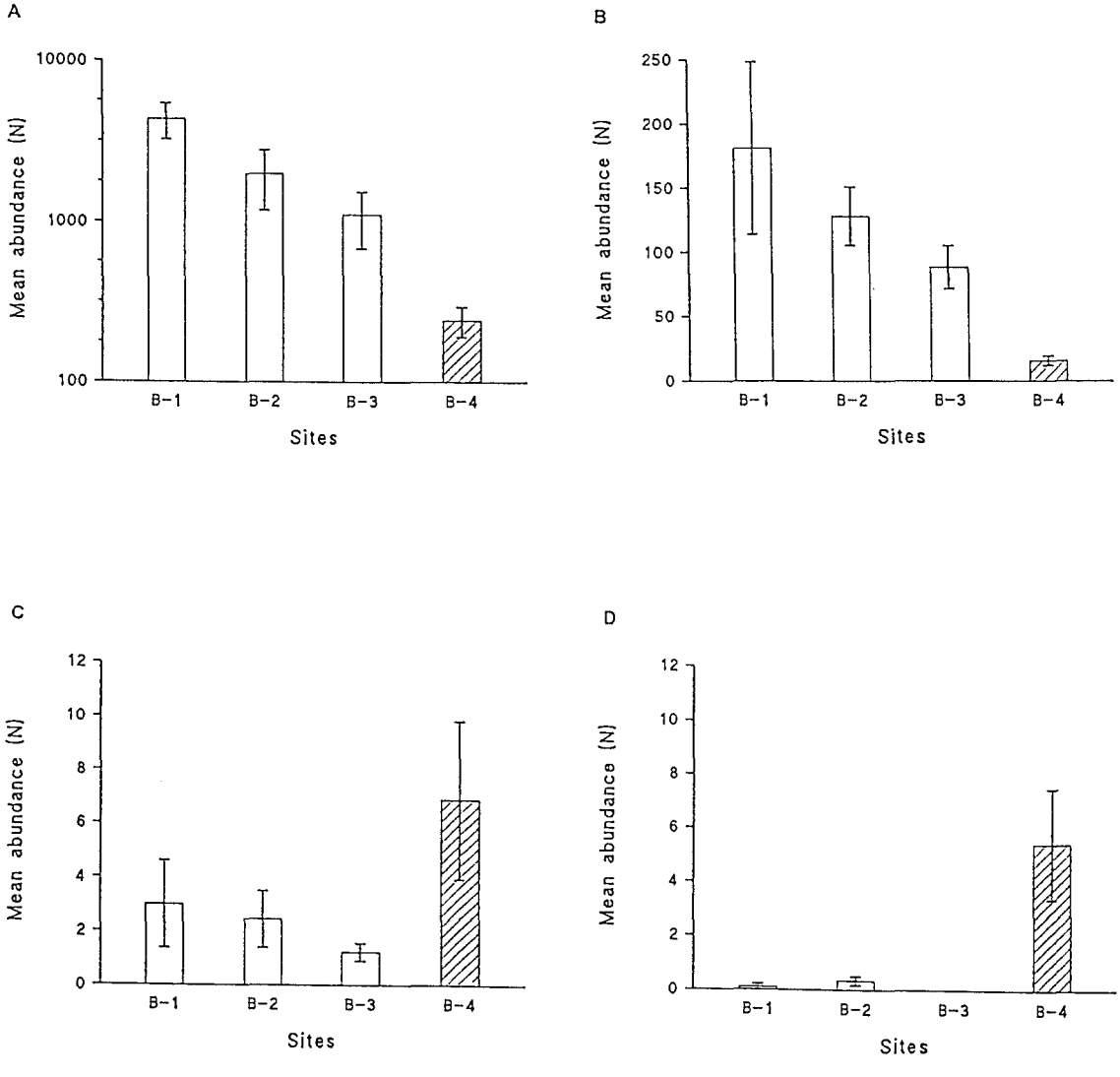

Figure 1. Abundance (numbers per week ±SE) of (a) Diptera, (b) Lepidoptera, (c) Thysanoptera and (d) Blattodea sampled from four beech tree crowns (n=9 weeks). B-1 to B-3 are honeydew trees, B-4 is the non-honeydew tree.

Table 1. The dominant Diptera in the four beech tree crowns. Sites 1 to 3 are honeydew trees, site 4 is the non-honeydew tree. All species described to genus or species level belong to the family Mycetophilidae

Site	Rank Dominance of Species 1	2	3	4	5
1	*Tetragoneura* sp.A	*Tetragoneura spinipes*	Dolichopodidae 1	*Anomalomyia guttata*	*Cycloneura* B
2	*Tetragoneura* sp.A	*Tetragoneura spinipes*	Ceratopogonidae 6	*Cycloneura* B	*Anomalomyia guttata*
3	*Tetragoneura* sp.A	*Tetragoneura spinipes*	Ceratopogonidae 6	*Mycetophila fagi*	*Tetragoneura rufipes*
4	Dolichopodidae 12	*Mycetophila subnitens*	*Tetragoneura* sp.A	Psychodidae 10	Ephydridae 2

patterns (Berger-Parker index (±SE) d=0.47±0.05 for honeydew trees, c.f. d=0.15 for B-4). The concordance of species ranking among sites was low (Kendall's coefficient of concordance, W=0.344; for 24 species of Diptera occurring 'dominantly' (i.e. in the top 10 most abundant species) in at least one of the four sites), and the pair-wise (Kendall's) rank correlation coefficients given in Table 2a show clearly that the same taxa were predominant in honeydew tree crowns, whereas other species were predominant in the non-honeydew tree community.

Coleoptera also exhibited a low concordance of ranking amongst sites (W=0.473), however the rank dominance of species on the non-honeydew tree was not clearly differentiated from that on honeydew trees (Table 2b).

Variation in community structure

As well as varying in species dominance, overall dipteran community composition and relative species abundances differed between honeydew trees and the non-honeydew tree. Mean faunal similarity (C_m) between honeydew tree crowns was high (mean (±SE) 82.79±2.26%), but mean similarity between honeydew trees and the non-honeydew tree was low (mean (±SE) 48.55±5.15%) (Student's t-test; T=6.09, p<0.01).

Ordination of all samples clearly showed the low faunal similarity of honeydew and non-honeydew dipteran communities (Fig. 2). The variation in site ranking explained by the first three DECORANA axes was 52.4%, 16.6% and 9.4%, respectively. Spring (November/December) and summer (January/February) samples formed separate clusters on DCA axes 1 and 2 (Fig. 2).

DISCUSSION

Preliminary data indicate that the canopy arthropod fauna on beech trees in the Blue Duck Scientific Reserve may be influenced by sooty beech scale honeydew secretions. Abundances of some insect groups were up to one order of magnitude greater on honeydew trees than on the non-honeydew tree. In particular, the dominant dipterans, *Tetragoneura* sp.A and *T. spinipes* (Mycetophilidae) were much more abundant on honeydew trees and may breed amongst the sooty mould fungi. The

Table 2. Kendall's rank correlation coefficients for pair-wise comparisons of species dominance: (a) rank correlation of 24 species of Diptera occurring 'dominantly' (i.e. in the top 10 most abundant species) in at least one of the four sites; (b) rank correlation of 23 species of Coleoptera occurring 'dominantly' in at least one of the four sites. Bold values indicate comparisons between honeydew trees and the non-honeydew tree. Other comparisons are between honeydew trees only. * = p<0.05. ** = p<0.01.

	A				B		
	B-1	B-2	B-3		B-1	B-2	B-3
B-2	0.7296**			B-2	0.5445**		
B-3	0.6043**	0.6270**		B-3	0.1601	0.4753**	
B-4	**-0.4583****	**-0.4748****	**-0.2365**	B-4	**0.3020***	**0.2501**	**-0.0188**

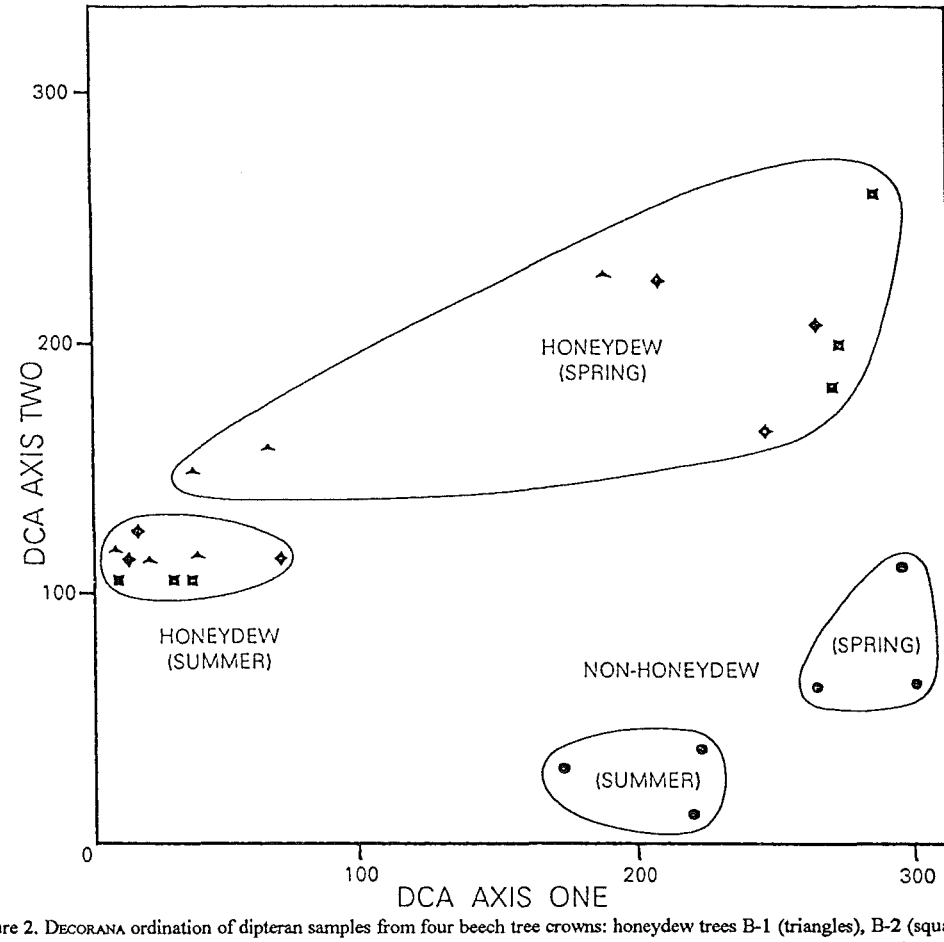

Figure 2. DECORANA ordination of dipteran samples from four beech tree crowns: honeydew trees B-1 (triangles), B-2 (squares) and B-3 (diamonds) and the non-honeydew tree B-4 (circles). Spring samples were from sampling weeks 1-3 (November/December 1990), summer samples were from sampling weeks 7,8 and 10 (January/February 1991).

non-honeydew tree fauna, however, was dominated by a predatory Dolichopodidae species. Although the proportion of insects that rely directly on honeydew as a food source is unknown (Boyd 1987, Moller & Tilley 1989), these abundance and species dominance data suggest that honeydew and associated fungal microhabitats significantly influence the arthropod fauna of beech trees. Honeydew may increase the food resource base for arthropods, availability of larval habitats, feeding and breeding sites for fungus-feeding arthropods, and refuges for certain species.

In contrast to the high abundance of some arthropod groups on honeydew beech trees, honeydew appeared to have a negative influence on the abundance of some other insect groups, notably Thysanoptera and Blattodea. This may be related to changes in tree morphology brought about by fungal mould growth on honeydew trees. Thysanoptera are typically flower or leaf feeders (Terebrantia; Mound & Walker 1982) or fungal feeders that live concealed beneath bark (Tubulifera; Mound & Walker 1986). In the canopy they may be associated with bark crevices or epiphytic plants. It is notable that epiphytes are almost completely absent from honeydew beech, because they are unable to colonize bark coated with sooty mould fungi. Open bark habitat is also extremely sparse on honeydew trees. These factors may account for the low abundance of Thysanoptera on honeydew trees. Similarly, Blattodea were significantly more abundant on the non-honeydew tree, perhaps associated with the tendency for many species to shelter in bark crevices (Johns 1966), although this has not been confirmed for the species present.

Overall composition of the insect groups stud-

ied varied markedly between honeydew trees and the non-honeydew tree. Faunal similarities of 30-50% indicate a high degree of heterogeneity in species composition, as emphasized by the DECORANA ordination. These differences are notable given the close proximity of the adjacent honeydew tree and non-honeydew tree (37 m) and the high vagility of most Diptera. Of interest, too, is the marked dichotomy of dipteran species composition between spring and summer (Fig. 2). The close grouping of two high-abundance/high-species richness spring samples from B-1 (triangles, Fig. 2) with the cluster of summer samples, indicated that the separation may be based on a seasonal increase in arthropod numbers, as well as possible changes in species composition.

In mixed canopy associations the presence of honeydew beech trees increases the overall diversity of arthropods present (Didham 1992), not only of beech dwellers, but also of other forest species for which honeydew may be a seasonal resource. In pure beech associations non-honeydew trees may also promote arthropod diversity because they provide an important habitat and food resource for certain bark and epiphyte dwelling species.

In the face of an invasion of introduced vespid wasps which utilise the honeydew resource heavily (Moller & Tilley 1989, Harris 1991, 1992, Moller *et al.* 1991), New Zealand beech arthropod communities may be undergoing significant changes in abundance and composition. It is likely that the native arthropod biomass in beech forests is greatly reduced by a lowering of the standing crop of honeydew. This is compounded by the detrimental effect of insect predation by wasps, calculated to be equivalent to the total dietary intake of the entire insectivorous bird fauna (Harris 1991, 1992). Of equal concern to the lowering of insect biomass in beech forests is the possible local extinction of arthropod species for which honeydew is required to meet specific energy requirements. Such species may fulfil critical roles in the functioning of forest ecosystems. While the eradication of wasps may not be an achievable goal, a reduction in wasp numbers may be essential for the maintenance of arthropod (and insectivorous bird) populations in beech forests.

Future research should focus on confirming these preliminary findings using replicated non-honeydew trees in pure beech forest, identifying which insect species rely directly on honeydew or associated fungal habitats, and determining the possible consequences of wasp predation and competition on the maintenance of community integrity in New Zealand honeydew beech forests.

ACKNOWLEDGEMENTS

I thank I. Didham, M. Tocher and Dr. D.A. Norton for help in the field, P.M. Johns for assistance with the identification of specimens and for providing guidance, and the Zoology Department, University of Canterbury for continued support during this study. M. Tocher, J. Harding and Professor M. Winterbourn provided useful comments on the script.

REFERENCES

Beggs, J.R. (1991). The Kaka (*Nestor meridionalis*), a New Zealand parrot endangered by introduced wasps and mammals. *Biological Conservation* 56: 23-38.

Belton, M.C. (1978). The place of beech scale insects (*Ultracoelostoma assimile*) in the ecology of mountain beech. MAF Honeydew Seminar, 10 August 1978. Christchurch, New Zealand, MAF Advisory Service.

Boyd, S.A. (1987). Patterns of use of honeydew by birds and insects. Unpublished M.Sc. thesis, University of Auckland, New Zealand.

Cook, V.A. (1971). Beech honeydew's export potential. *New Zealand Journal of Agriculture* 122: 51.

Crozier, L.A. (1978). Honeydew resource of the Oxford State Forest. MAF Honeydew Seminar, 10 August 1978. Christchurch, New Zealand, MAF Advisory Service.

Crozier, L.R. (1981). Beech honeydew: forest produce. *New Zealand Journal of Forestry* 26: 200-209.

Didham, R.K. (1992). Faunal composition, diversity and spatial heterogeneity of the arboreal arthropod community in a temperate rain forest canopy, New Zealand. Unpublished M.Sc. Thesis, Zoology Department, University of Canterbury.

Gaze, P.D. & Clout, M.N. (1983). Honeydew and its importance to birds in beech forests of the South Island, New Zealand. *New Zealand Journal of*

Ecology 6: 33-37.

Grassle, J.F. & Smith, W. (1976). A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia (Berl.)* 25: 13-22.

Harris, R.J. (1991). Diet of two wasps *Vespula vulgaris* and *V. germanica* in honeydew beech forest of the South Island, New Zealand. *New Zealand Journal of Zoology* 18: 159-169.

Harris, R.J. (1992). Competition between the introduced wasps *Vespula germanica* and *V. vulgaris* in honeydew beech forest north-western South Island, New Zealand. Unpublished Ph.D. thesis, Zoology Department, University of Canterbury, Christchurch, New Zealand.

Harris, R.J., Thomas, C.D. & Moller, H. (1991). The influence of habitat use and foraging on the replacement of one introduced wasp species by another in New Zealand. *Ecological Entomology* 16: 441-448.

Hill, M.O. (1979). DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University Ithaca, New York.

Horn, H.S. (1966). Measurement of "overlap" in comparative ecological studies. *The American Naturalist* 100: 419-424.

Hughes, S.J. (1972). New Zealand Fungi 17. Pleomorphism in Euantennariaceae and Metacapnodiaceae, two new families of sooty moulds. *New Zealand Journal of Botany* 10: 225-242.

Johns, P.M. (1966). The cockroaches of New Zealand. *Records of the Canterbury Museum* 8(2): 93-136.

Kelly, D. (1990). Honeydew density in mixed *Nothofagus* forest, Westland, New Zealand. *New Zealand Journal of Botany* 28: 53-58.

Kelly, D., Stirling, D.J., Hunt, G.R., Newell, C.L. & Jarvis, C.E. (1993). Honeydew standing crop and production over 24 hours in *Nothofagus solandri* forest in Canterbury. *New Zealand Journal of Ecology* 16(2): 69-75.

McAllum, P. (1992). Interactions of the scale insect and Kaka in South Island beech forest. Unpublished B.Sc.(hons.) project, Zoology Department, University of Canterbury, New Zealand.

McCune, B. (1991). Multivariate analysis on the PC-ORD system. Oregon State University, Oregon.

Moller, H., Clapperton, K., Gaze, P.D., Sandlant, G., Thomas, B.W. & Tilley, J.A.V. (1987). Honeydew life blood of South Island beech forests. *Forest and Bird* 18: 14-16.

Moller, H. & Tilley, J.A.V. (1987). Honeydew, a South Island beech forest resource. *Alpha* 58. Wellington, DSIR Publishing.

Moller, H. & Tilley, J.A.V. (1989). Beech honeydew: seasonal variation and use by wasps, honeybees and other insects. *New Zealand Journal of Zoology* 16: 289-302.

Moller, H., Tilley, J.A.V., Thomas, B.W. & Gaze, P.D. (1991). Effect of introduced wasps on the standing crop of honeydew in New Zealand beech forests. *New Zealand Journal of Zoology* 18: 171-179.

Morales, C.F., Hill, M.G. & Walker, A.K. (1988). Life history of the sooty beech scale in New Zealand *Nothofagus* forests. *New Zealand Entomologist* 11: 24-37.

Morisita, M. (1959). Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E, Biology* 3: 65-80.

Mound, L.A. & Walker, A.K. (1982). Terebrantia (Insecta: Thysanoptera). *Fauna of New Zealand* no. 1.

Mound, L.A. & Walker, A.K. (1986). Tubulifera (Insecta: Thysanoptera). *Fauna of New Zealand* no. 10.

Taylor, R.H. (1985). Status, habits and conservation of *Cyanorhamphus* parakeets in the New Zealand region. *International Council for Bird Protection, technical publication* no. 3: 195-211.

Wardle, J.A. (1971). The forests and shrublands of the Seaward Kaikoura Range. *New Zealand Journal of Botany* 9: 269-292.

Wardle, J.A. (1984). *The New Zealand beeches: ecology, utilization and management.* New Zealand Forest Service, Wellington.

Wardle, P. (1961). The forest of Aniseed Stream near Kaikoura. *New Zealand Journal of Forestry* 8: 477-481.

Wolda, H. (1981). Similarity indices, sample size and diversity. *Oecologia (Berl.)* 50: 296-302.

Wolda, H. (1983). Diversity, diversity indices and tropical cockroaches. *Oecologia (Berl.)* 58: 290-298.